UTRICULARIA: ITS DEVELOPMENT FROM THE SEED.

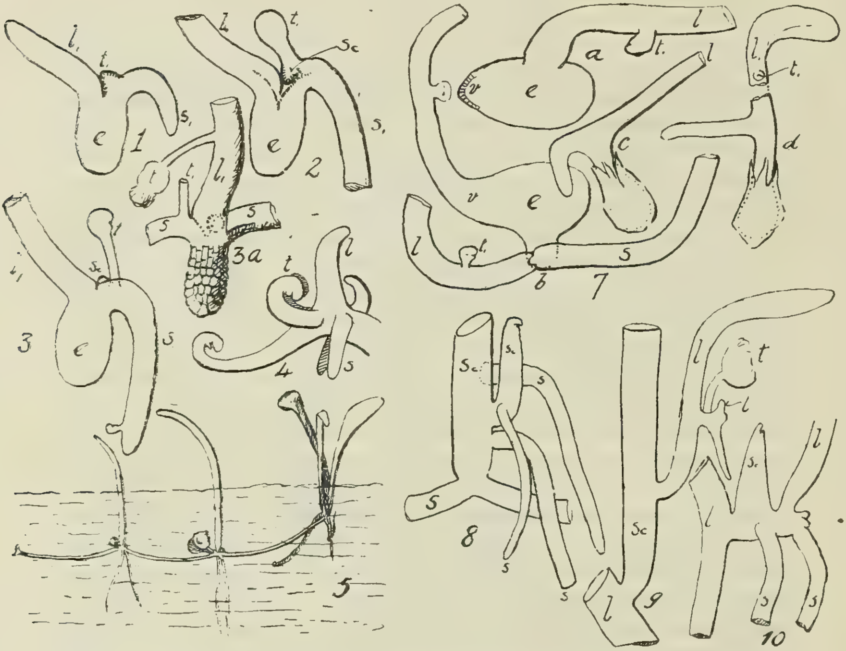
(With Plate 27.)

By Francis E. Lloyd.

Utricularia, together with Polypompholyx and Biovularia, genera of doubtful standing, consists of plants which are in many respects unique in their morphology. The many attempts to assimilate them in this respect with plants in general—that is, to find root, stem and leaf—were disposed of by Goebel, the foremost student of his time of the group. Without setting forth a summary of the controversy, we may say briefly (1) that there is no root ; (2) there is a stem which is the scape of an inflorescence, that rises secondarily from the body of the plant ; (3) this plant body, which differentiates itself into " leaf," " stem," "stolons " and " bladders," complicated as this becomes in some cases, is in its entirety of leaf nature. It is only when this point of view is adopted—with indeed what scepticism seems indicated—that anything like a rational description of the plant body becomes possible. The conventional definition of " leaf," the product of the older formal morphology, does not hold ; we have to describe what a leaf does physiologically rather than what it is. It is of unlimited growth and produces " leaves," " stems," organs which appear to be neither leaf nor stem, but which for a better term we call " stolons," special " shoots " (*e.g.*, the air shoots described by Goebel, in many floating species), " tubers " which completely violate the accepted definition of these organs, etc. The terms are put into quote-marks, since while used (in the lack of an entirely new terminology) they must be used in a physiological and in no strict morphological sense. A realization of the fundamental facts can be come by best by following the ontogeny of the plant beginning with the mature seed, though the inquiry might well begin with the early embryo, for something happens during its course of development which robs it of a root, so that the embryo as we find it in the seed lacks this organ entirely. (For information about the embryology one should read Merz, Merl and Lang.)

The species of Utricularia fall into two main groups of physiological import, (1) those which are more or less freely floating but submersed either totally (*U. flexuosa*), or with the upper surface of the leaves exposed

(*U. intermedia*), and (2) those which are always anchored in a substrate, loose or compact, but supplied with an abundance of water of greater or less permanence. In these latter the leaves may be large and of complex structure (*e.g.*, *U. reniformis*) reaching up into the air ; or may be small and scarcely rising above the surface of the substrate, and with simple structure. According to the duration of water supply of the habitat, these species may be evanescent, or of more or less protracted



Figs. 1-3. Successive stages in the germination of the embryo of *U. capensis : e*, embryo ; *l*, leaf ; *s*, stolon ; *t*, trap. 3a. An abnormal case (*U. capensis*) in which three organs (a leaf and two stolons) arose simultaneously from the growing point of the embryo. 4. The organs at the node of a running stolon in *U. monanthos : t*, trap ; *l*, leaf ; *s*, stolon. 5. *U. monanthos*, showing the habit of a young plant. Habitat : mud with water above. 7. Various behaviours during germination in *U. bifida : a*, Leaf produced on the flank of the seed instead of at vegetation apex (*v*) ; *b*, leaf only at vegetation apex and protuberance bearing leaf and stolon produced laterally ; *c*, vegetation apex grows into a mass bearing stolon and leaf without evident distinction at the base ; *d*, the primary leaf produces the primary stolon. 8. *U. capensis :* A scape has arisen from a stolon and from it a secondary scape and stolons have arisen : *sc*, scape ; *s*, stolons. 9. *U. capensis :* A scape has arisen from a leaf, and from the scape a leaf with a bud bearing leaf, trap and stolon : *l*, leaf ; *sc*, scape ; *t*, trap. 10. Similar to fig. 9, but the scape arises from a complex bud.

growth and generally of small size. Strict annuals or facultative or true perennials occur among these.[1] Of those species presenting a brief life cycle, the most striking known to me is Polypompholyx (Utricularia) of which two species *multifida* and *tenella* are recognised. The plants grow during the rainy season (winter rains) in temporary sandy swamps which on the on-coming of drought become quite dry. Seedlings were found near Perth in July, 1936 (under the guidance of Mrs. Eileen R. L. Johnson) with three to five leaves and as many or more traps, with the seed coat still attached to the embryo. From this material I am able to draw an account which I venture to believe is fairly correct. It will serve as a point of departure, as the simplest type from the developmental point of view of all.

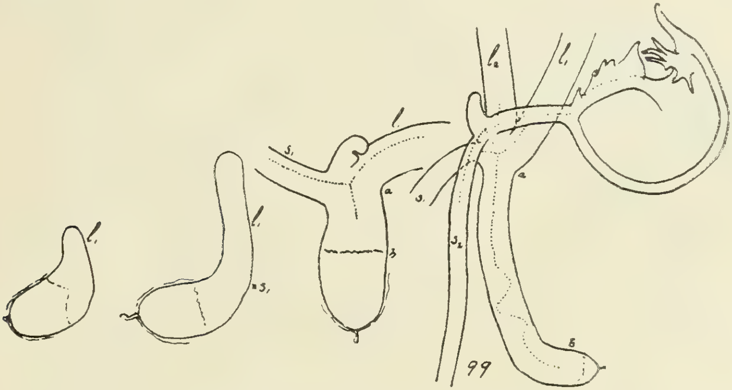


Fig. 6. Germination in *U. monanthos*.

Abrupt Development.

The embryo is a rounded mass (ca. 0·2 mm. in diam.) somewhat concave on the root pole. The shoot pole is undifferentiated, it being clothed with simple columnar epidermal cells, with no prominences to indicate future organs. At an early stage of germination(2) two prominences appear (as in fig. 1), one of which elongates to form the first leaf; the other elongates similarly, but with downward growth, to form a colourless stolon. I call these "cotyledonoids" (figs. 11, 12). At the apex of the embryo between these two organs *there is no vestige of apical growth* and none is seen hereafter. The next definite step is the growth

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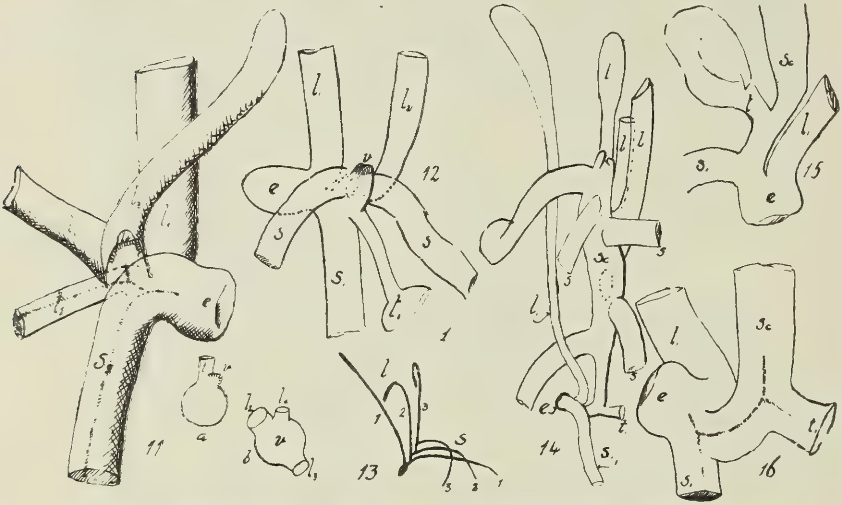
(1) The taxonomic group "Natantes," often recognised, has no morphological value, though it may be useful in an artificial key.

(2) Seed sent me by Mrs. Johnson supplied earlier stages of germination.

of the first trap, which arises near the base of the stolon and a little on one side (figs. 11, 12). From a point at or near the juncture of the stalk of the trap and the stolon from which it sprung arises a second swelling from which develops an axis growing vertically upward (figs. 14-16). In the vast majority of cases this axis is not distinguishable from its lateral organs ; but in about 5 per cent. of the seedlings, it elongates as if etiolated (fig. 14). It can then be seen to bear stolons, leaves and traps in no obvious order. The axis becomes thicker towards the growing apex about which new stolons, etc., are formed until at length a terminal scape is produced. The radial axis and the stolons which have arisen produce traps which are of two kinds : large ones on short stolons near the surface of the substrate, and small ones on longer stolons usually penetrating deeply. The size of the large traps relatively to that of the plantlet is quite enormous. No runner stolons are produced.



Figs. 11. Polypompholyx. Young protocorm produced at the base of the primary trap, on the base of the primary stolon : *t*, trap ; *s*, stolon ; *e*, embryo ; *l*, leaf ; l_3 must be regarded as transparent : *a*, diagram, section of primary stolon to show relative positions of first trap and protocorm ; *b*, positions of leaves 2-4 on the protocorm (approx.) ; *v*, growing point of protocorm. 12. *U. capensis* : The same relations as seen in fig. 11. 13. Diagram to show succession of leaves and stolons in a seedling of *U. bifida*. 14. Somewhat advanced seedling of Polypompholyx ; *sc*, protocorm which at length ends in a scape. 15. The basal portion of a similar seedling of Polypompholyx to show the protocorm united with the stalk of the primary trap, and both arising from the primary stolon. 16. Detail of the seed region of fig. 14.

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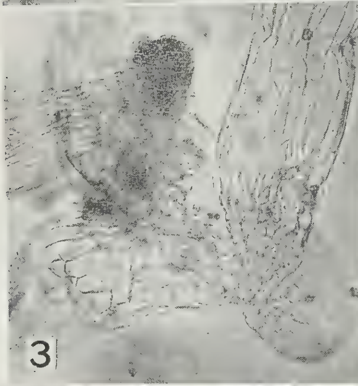
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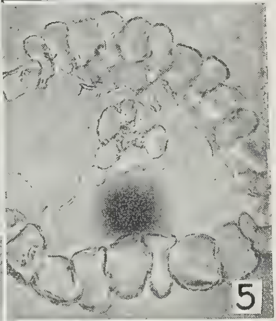
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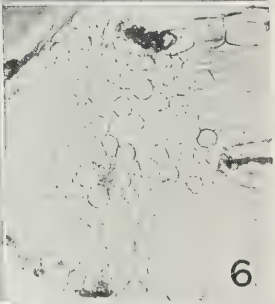
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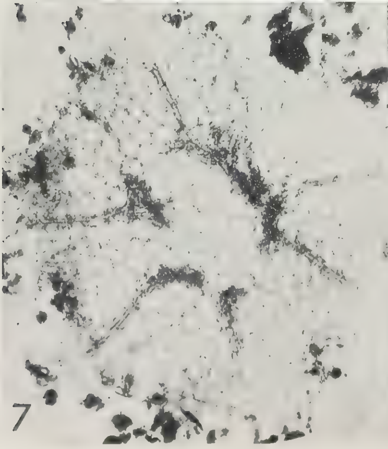
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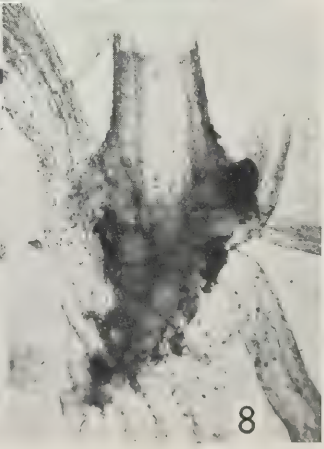
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Plate 27

A question must now be asked, namely, what is the morphological nature of the axis. When it first arises it seems to be identical in structure with that of a stolon. Its origin is the same and cannot be distinguished from that of the stolon or a trap, and is often concrescent or fasciated with the stalk of the first trap (fig. 15). It has only a single strand of vascular tissue, with a single spiral vessel. As lateral organs (stolons, traps or leaves, in no recognizable order) appear, strands, branches of the central, are given off, one to each. As maturity of the plant is reached, the axis, at first composed of delicate parenchyma, becomes somewhat more compact, the whole becoming corm-like in aspect (Plate 27, figs. 7, 8). The central strand gradually spreads out by means of branches to form a sort of central cylinder, but the structure is loose and ill-defined. Only when the scape is formed at the apex does the vascular tissue render the whole stem-like. We may say therefore that an organ at first not distinguishable from a stolon gradually assumes the character of a true stem.

The above account is applicable also to *U. violacea*.

It is a puzzling question as to the nature of the embryo. There seems to be no portion of it which constitutes a stem meristem. The evidence indicates that there is none, and that any area of the whole embryo is capable of producing the initial organs, stolon and leaf. I have found embryos of *U. bifida* which behave in this way (fig. 7).

The above method of development may be described as " abrupt," since the plantlet proceeds at once, after the original organs are laid down, to form an axial organ, the corm we may call it, which terminates in a floral scape.

In some species (*U. Menziesii*, *U. volubilis* and others ?), this corm is perennial. Although definite evidence is lacking it seems highly likely that it arises as it does in Polypompholyx. In *U. Menziesii*, the corm is upright. The tapering basal portion dies off, and it grows at the upper pole, giving off numerous traps, stolons, leaves, scapes and tubers. The latter may be regarded as water storage organs. The plant grows in the same sort of habitat as Polypompholyx, in a loose sandy substrate.

PLATE.

Plate 27.—1. *U. capensis* : Young stage of germination. 2. Somewhat later stage of germination : *U. capensis*, cf. text figs. 1-3. 3. The protocorm has taken form ; it is seated on the primary stolon. *U. capensis*. 4. Runner-stolon, *U. capensis* : near the left end a new scape will arise. 5. Transverse section, leaf base, *U. capensis* : large intercellular space in which the vascular strand is suspended by a small amount of chlorenchyma. 6. Transverse section through the lower part of a protocorm of Polypompholyx. 7. Traverse section of a mature corm of Polypompholyx. 8. Mature corm of Polypompholyx, with base of scape : a second scape is forming on the right.

DIFFUSE DEVELOPMENT.

When, however, instead of producing a scape, other organs, leaves, stolons, traps, only are formed, the scape being produced adventitiously from a stolon, such behaviour may be termed diffuse. In some species, however, a scape is developed at once, and further stolons extensive in function, leaves, etc., arise secondarily. It is very difficult to get material of suitable stages for examination of this point. However, that of *U. monanthos*, grown for me at the Edinburgh Botanic Garden, supplies the evidence for that species.

U. monanthos—The germinating embryo elongates at one pole, the whole elongation becoming a leaf from which then, near its base, a stolon emerges (fig. 6). From this, near the leaf base but not quite in the middle line, a trap grows, accompanied somewhat later by a stolon. The growing mass of tissue which gives rise to the trap enlarges to accomplish this, until a definite bud is formed which may take on the character of a corm ; and while it is doubtful if a scape arises from it, it would be no surprise if it occasionally did so.

It is clear that this bud arises secondarily from the first stolon, not directly from the embryo (agreement with Polypompholyx). From this, as a focus, arises a stolon which becomes a major axis, creeping horizontally through the substrate (fig. 5). Others arise later. On the stolon at nodes arise in definite order the usual complement of organs, a single leaf, median above in position, traps and stolons in pairs, a second median organ being probably a leaf (fig. 4). This is the general scheme, further study being required to trace definitely the fate of all buds. In this plant, as Goebel pointed out for *U. orbiculata*, the upper face of the leaf is addressed towards the original axis and not towards the apex of the stolon which bears it, as if the stolon itself were but the leaf stalk capable of proliferating. This is rather surprising. It means that the original orientation or polarity is not lost. The stolon is not a branch in the accepted morphological sense. Nor is its anatomy more helpful, for there is but a single delicate strand of vascular tissue with one, perhaps two, spiral vessels running along the upper side of the phloem.

U. capensis—The course of events is the same for *U. capensis*, only that in this species (*a*) there is always normally produced a scape directly from one of the cotyledonoids of the embryo, as described for Polypompholyx, and from the base of this new scapes may arise adventitiously as in fig. 8 ; and (*b*) from the protocorm, running stolons originate to give rise to secondarily produced scapes (fig. 8), and this may continue as long as wet habitat conditions persist. The production of stolons may often precede that of the scape. I found in August 1929 on Table Mountain a bed of moss with a few leaves of *capensis* showing. On carefully pulling the substrate apart later I found seedlings in various stages, most of which however already showed a young scape, and all with several long running stolons with many traps (Plate 27, fig. 4). The running stolons bear leaves at intervals, but there is no definite plan of arrangement followed by the traps and stolon branches (as in *U. monanthos*). Stolon branches are usually lateral ; traps occur from any point, though chiefly lateral (Plate 27, figs. 1-4 ; text figs. 1-3, 9, 12).

But the course of development from cotyledonoid to scape is not always as direct as above described. Seedlings of *U. bifida* showed the following behaviour. The first stolon arises from the base of the first leaf. This relation is alternative with the condition that both arise simultaneously from the embryo (fig. 7). In the former case we probably have to do with the elongation of the embryo below the level of origin of the cotyledonoids ; but in any case the leaf appears first. From near the base of the first stolon arises a second leaf, which later emits a stolon near its base, this sequence to be repeated for some time. The scheme is set forth in the diagram herewith (fig. 13).

In Polypompholyx, *U. violacea*, *U. capensis*, the protocorm normally arises in the position of leaf 2 in this diagram ; but occasionally (in nature) the process may be delayed, the individual following the above scheme. Here also it should be noted that in the position of leaf 2, a trap only may arise at first, another organ (protocorm or other) arising from a vegetation point at its base.

Little light can be got concerning these sequences except by direct observation of the growing plants. The above descriptions are based on such observation. Heretofore no exact account of these relations has been published. Kamienski made a drawing of an early stage (only the two cotyledonoids and a trap showing) of *U. lateriflora* (Engler and Prantl). Goebel examined the seedlings of two species, *U. bifida* and *U. elachista*. The youngest stages only of the former were seen. His illustrations show clearly that he recognised that a new organ appears at the base but not on the middle line of the primary stolon,(1) it being regarded as a radially constructed organ, and called by him a "shoot vegetation point," but as he did not follow its development his interpretation is open to question. He makes the guess that it ends in forming the inflorescence ; but I have found that it develops into the second leaf

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(1) I find that I misrepresented Goebel's view in my review paper (Lloyd 1935, bottom of page 74 and top of page 75), and the footnote was robbed of its meaning by the use or "former" for "latter." What Goebel seems to have meant is that the vegetation point appears first between the "cotyledons" and later on the base of the stolon presumably by elongation of this organ at the base. If I now represent Goebel correctly, I think he was mistaken.

(in *U. bifida*), while in Polypompholyx a trap, followed at its base by a radial structure which ends in a scape, is formed. I have found evidence to suspect that seedlings grown under unnatural conditions do not always behave quite usually, and Goebel's interpretation may well be true for naturally grown seedlings, though evidence is wanting on this point. Of *U. elachista* Goebel saw only a " seedling " which had as a matter of fact become a mature plant (as it bore a flower) and the steps of development were no more to be traced. He says indeed that the germ-shoot is radial, but he does not and could not have traced its origin in his material. Nor does he tell us about the vascular structure, this being such as to halt us when we incline to say radial.

UTRICULARIA CAPENSIS.

Since in the Cape Province we are particularly interested in *U. capensis*, we shall extend our description of this species in some detail. The embryo, which is oval (ca. 0·2 × 0·3 mm.), normally produces during germination, raised on an extended upper zone (the upper half of the embryo lengthens) (Plate 27, fig. 1) two cotyledon-like structures ("cotyledonoids "), one of which growing upwards becomes a leaf, the other, growing initially downwards, a stolon (text-figs. 1-3). On the stolon near its base but not quite in the middle line appears the first trap (Plate 27, fig. 1, and text-fig. 1). From a growing point which occurs partly on the base of the trap stalk and partly on the stolon a radial structure, the protocorm, (Plate 27, fig. 2, and text-fig. 3) develops. Whether this growing point arises *de novo* or is a persistent portion of the original growing point which gave rise to the first trap, cannot at the moment be said ; and this question applies equally to other species above considered. It is important to note that the size of the trap stalk overshadows that of the growing point (Plate 27, fig. 2, and text-fig. 2), and this may have confused the issue. This disparity of size between the growing point and the lateral organs springing from it is a constant feature peculiar to these plants, and makes difficult a clear picture on dissection.

The procedure above presented is not always followed. Abnormal germinations occur which are not without interest, since they illustrate a high degree of plasticity possessed by Utricularia. Among seedlings grown in living Sphagnum in a vial I obtained one in which three initial organs were produced, a leaf and two stolons, set in a triangle much as in the case of *U. emarginata*, one of the Natantes (Goebel). From one stolon the first trap was produced, from the leaf later several others, and at its base there is a growing point which appears to be the corm (fig. 3a).

It may, however, be intended as a stolon, and there is no way of deciding. The germination of Utricularia offers a wide and interesting field for observation.

The protocorm must be regarded as radial (Plate 27, figs. 1-3, 6-8), As it develops it produces from all sides leaves and stolons which travel out, spreading in the substrate, and from them arise leaves, facing the origin, not the apex, of the bearing stolon (Plate 27, fig. 4). The bud elongates and at the same time thickens to form a corm which bears leaves and stolons and at length a scape, the primary. From its base, without a bract, and partly or wholly from the top of the corm, a second and even third scape may arise. Secondary scapes arise also from the upper surface of the running stolons and from leaves (figs. 8-10), and in this way the period of flowering is prolonged indefinitely. With the guidance of Mr. Middlemost it was found growing and profusely flowering on wet rocks in Bain's Kloof on March 8, 1936, long past the season in places subject to drought.

The body of the corm is composed of a very soft, spongy parenchyma of globose cells held together by short bridges, the whole having little mechanical strength (Plate 27, fig. 6). The epidermis is very frail and the surface is broken up by the numerous bloated stolons, traps and leaf-bases. The bloating is owing to the extensive intercellular spaces, so that stolons and leaves are little more than tubes traversed by a single vascular strand. In corm, leaf and stolon this vascular strand is asymmetric, for if xylem is present it occupies a position on one side of the phloem. In the corm there is at first only a single central vascular strand (Plate 27, fig. 6), its asymmetric character detracting from the perfect symmetry of a radial organ. As the corm develops it becomes larger, and the vascular strands tend to travel outward more and more in order to enter the lateral organs. As the upper regions of a mature corm are reached the strands have spread out so as to form an irregular circle of about six or seven groups of vessels (Plate 27, fig. 7), but without any striking order or symmetry. Only when the definitive scape is reached is there any great measure of radial symmetry attained. Here the phloem and xylem travel more or less independently, as Hovelacque long ago showed.

Stolons and leaves have the same structure aside from the secondary features of palisade tissue, etc. (Plate 27, fig. 5). A single vascular strand only is present and the xylem is always above the phloem and not, as one would expect, below. This is only one of the paradoxes presented by these peculiar plants.

Both leaves and stolons are beset with traps (Plate 27, fig. 4) which occur, in contrast with the condition in *U. monanthos*, quite irregularly, scattered along the flanks and upper surface, and on the edges or backs of leaves.

The purpose of this paper, to furnish an account of the origin of the various organs in relation to the embryo, has been accomplished. The chief point to be emphasized is that the origin of a " radial " structure, which produces various organs, but at length a flowering scape, is secondary in that the point of origin is on and near the base of the primary stolon which holds the position of a cotyledon.

No consideration has been given to the so-called " Natantes," meaning here the *U. vulgaris* group, studied by Kamienski, Warming and Merl, for the reason that the facts are well known while the institution of a comparison of these with those forms which have been here examined would involve a lengthy discussion beyond the scope of our purpose.

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